

**TWO NEW SPECIES OF *RHAGOVELIA* FROM THE PHILIPPINES,
WITH A DISCUSSION OF ZOOGEOGRAPHIC RELATIONSHIPS
BETWEEN THE PHILIPPINES AND NEW GUINEA
(HETEROPTERA: VELIIDAE)**

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Abstract.—Two new species of *Rhagovelia* are described from the Philippines: *R. ridicula* from Mindanao, Leyte, and Luzon, and *R. phoretica* from Negros. *R. ridicula* belongs to the *orientalis* group as defined by Polhemus and Polhemus (1988), being the apparent sister species to *R. aberrans* Andersen, while *R. phoretica* belongs to a distinctive intrageneric clade defined herein as the *caesius* group, whose only other members occur on New Guinea. The male paramere of *R. weneri* Hungerford and Matsuda is figured, and its structure is shown to be correlative to that of a monphyletic group of species occurring on New Caledonia and in the highlands of New Guinea, thus supporting the placement of this species in the *novacaledonica* group of Polhemus and Polhemus (1988). The evidence of a sister area relationship between the Philippines and New Guinea as indicated by the disjunct distributions of taxa in the *caesius* and *novacaledonica* species groups is discussed, and possible tectonic mechanisms that could have led to such a disjunction are evaluated.

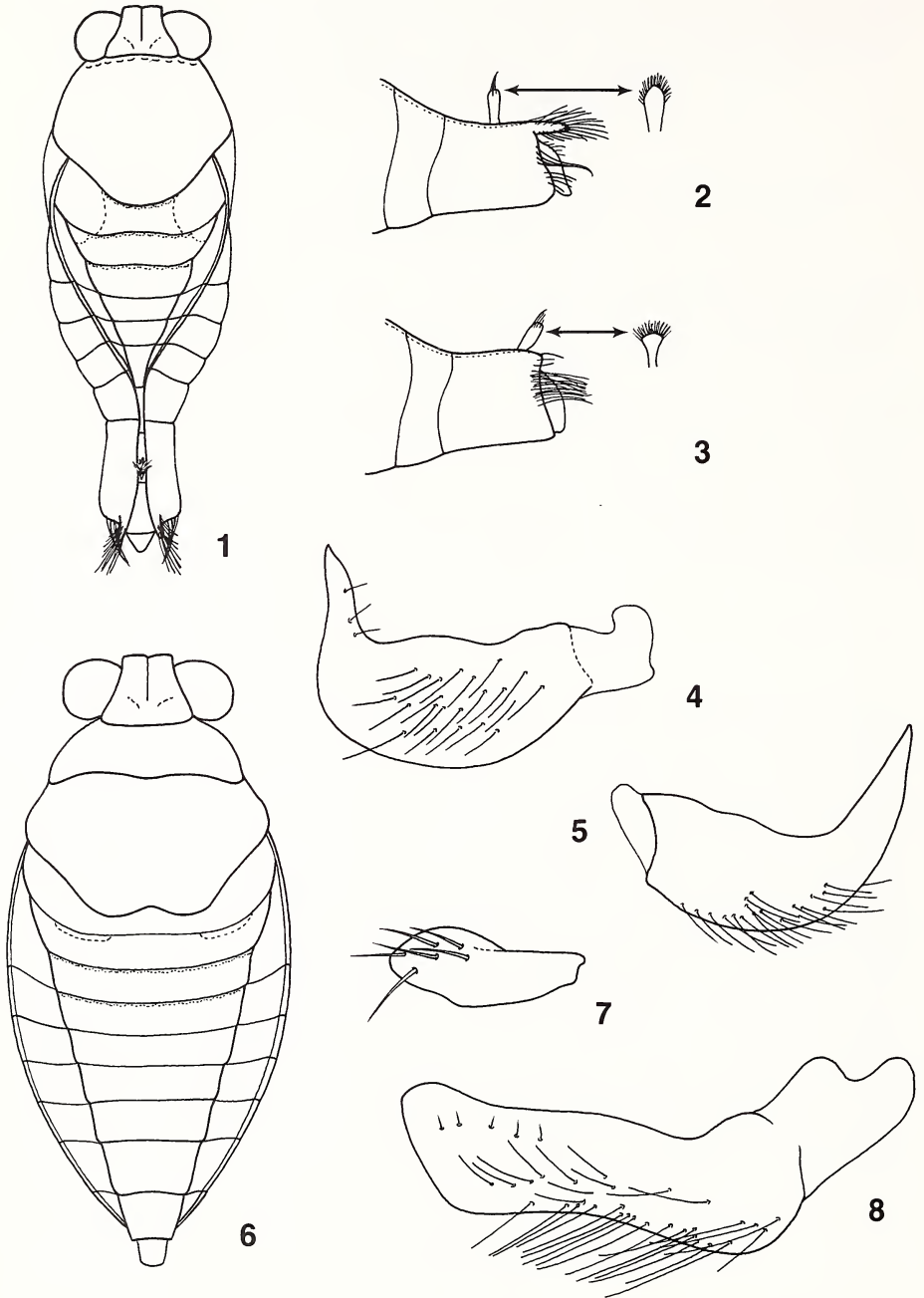
Seventeen species of *Rhagovelia* were described from the Philippines prior to 1993 (Lundblad, 1936, 1937; Drake, 1948; Hungerford and Matsuda, 1961; Andersen, 1965; Polhemus and Reisen, 1976). Of these, *R. hoberlandti* Hungerford and Matsuda has proved to be a synonym of *R. kawakamii* (Matsumura) (Polhemus and Reisen, 1976), *R. teretis* Drake a synonym of *R. luzonica* Lundblad, and *R. mindanaoensis* a synonym of *R. orientalis* Lundblad (Polhemus and Polhemus, 1989), leaving fourteen valid names. Many additional species are present, including the two new taxa described herein, and a synthetic revision of the Philippine *Rhagovelia* fauna currently in preparation by Herbert Zettel of the Naturhistorisches Museum Wien, Austria, will raise the total even further. Polhemus and Polhemus (1988) discussed the overall composition of the Philippine *Rhagovelia* fauna in the context of species groups they had proposed, and commented in passing on the zoogeographic affinities of these taxa. This present paper amplifies on that work, providing descriptions of several new species important to the zoogeographical comprehension of the region, and discussing in greater detail the faunal disjunctions between the Philippines and New Guinea seen in certain *Rhagovelia* species groups, and the tectonic mechanisms that may have produced such patterns.

TAXONOMY

***Rhagovelia ridicula*, new species**

Figs. 1, 2, 5, 9

Diagnosis: Similar to *R. aberrans* Andersen, but distinguished by the differing shape and placement of the erect process arising from female abdominal tergite VII (compare Figs. 2 and 3), and the shape of the male paramere (compare Figs. 4 and 5).



Figs. 1-8. 1. *Rhagovelia ridicula* n. sp. Wingless female, dorsal habitus, legs omitted. Specimen from Cabigaan River, Leyte. 2. *Rhagovelia ridicula* n. sp. Lateral view of female terminal abdomen, showing location and structure of vertical process. 3. *Rhagovelia aberrans*

Description:

Wingless male: Form narrow and elongate, length 2.88 mm; maximum width (across posterior section of pronotum) 1.08 mm. General dorsal coloration dark grey; anterior portion of pronotum with frosty grey transverse band, extending downward onto pleural area; small dark orange spot centrally on anterior portion of pronotum behind head; genital segments black.

Head dark grey, eyes black, frons and vertex bearing scattered stiff dark setae; antennae black, all segments of relatively equal thickness, segment I pale yellow on basal 1/4, all segments covered with very short semi-recumbent dark pubescence, segment I also bearing 6–7 long stiff erect black setae, 1–2 setae of this type also present near middle of segment II; lengths of segments I–IV = 0.76, 0.40, 0.44, 0.44; proepisternum and jugum lacking black denticles.

Pronotum dark grey, anterior 1/4 frosty pruinose grey, length/width = 0.80/0.92, completely covering mesonotum, length of exposed metanotum at midline = 0.10; anterior pronotal lobe bearing small ovate dark orange spot behind head vertex, appearing diffuse due to overlying pruinosity; pronotal surface covered with short recumbent pale setae, these setae longer on posterior margin; disk not distinctly foveate, bearing only scattered, very small, deep pits.

Abdomen dark grey overlain with faint silvery pruinosity, tergite I longer than II (0.16), II–V equal in length (0.12), VI–VIII progressively longer (0.16, 0.20, 0.36 respectively); all tergites and connexival segments covered with short to moderate length semi-recumbent pale setae, connexival margins evenly tapering and convergent along their entire lengths.

Legs black, with margins of acetabulae adjoining coxae yellowish brown; all segments thickly covered with short recumbent pale setae; trochanters unarmed; fore, middle and hind femora and tibiae with scattered long erect stout black setae along anterior margins; fore femur with scattered slender erect black setae along posterior margin; fore tibia simple and cylindrical, not bent or expanded; middle femur unmodified, cylindrical, tapering, bearing a line of long slender erect black setae along posterior margin; middle tibia slender, cylindrical; hind femur and tibia with scattered long fine erect brown setae along posterior margins; hind femur very weakly incrassate, bearing a small black spine on posterior margin near middle, followed by 2–3 much smaller black spines; hind tibia straight, cylindrical, with small tuft of semi-erect black setae along anterior margin on distal 1/3.

Proportions of male legs as follows: fore femur/tibia/tarsal 1/tarsal 2/tarsal 3 = 0.92/0.88/0.03/0.04/0.20; middle femur/tibia/tarsal 1/tarsal 2/tarsal 3 = 1.60/1.20/0.04/0.68/0.64; hind femur/tibia /tarsal 1/tarsal 2/tarsal 3 = 1.28/1.40/0.04/0.04/0.28.

←

Andersen. Lateral view of female terminal abdomen, showing location and structure of vertical process. 4. *Rhagovelia aberrans* Andersen. Male paramere. Specimen from Ayala River, Mindanao. 5. *Rhagovelia ridicula* n. sp. Male paramere. Specimen from Sapa River, Mindanao. 6. *Rhagovelia phoretica* n. sp. Wingless female, dorsal habitus, legs omitted. Specimen from Amulan, Negros. 7. *Rhagovelia phoretica* n. sp. Male paramere. Specimen from Amulan, Negros. 8. *Rhagovelia werner*i Hungerford and Matsuda. Male paramere. Specimen from Mt. Apo, Mindanao.

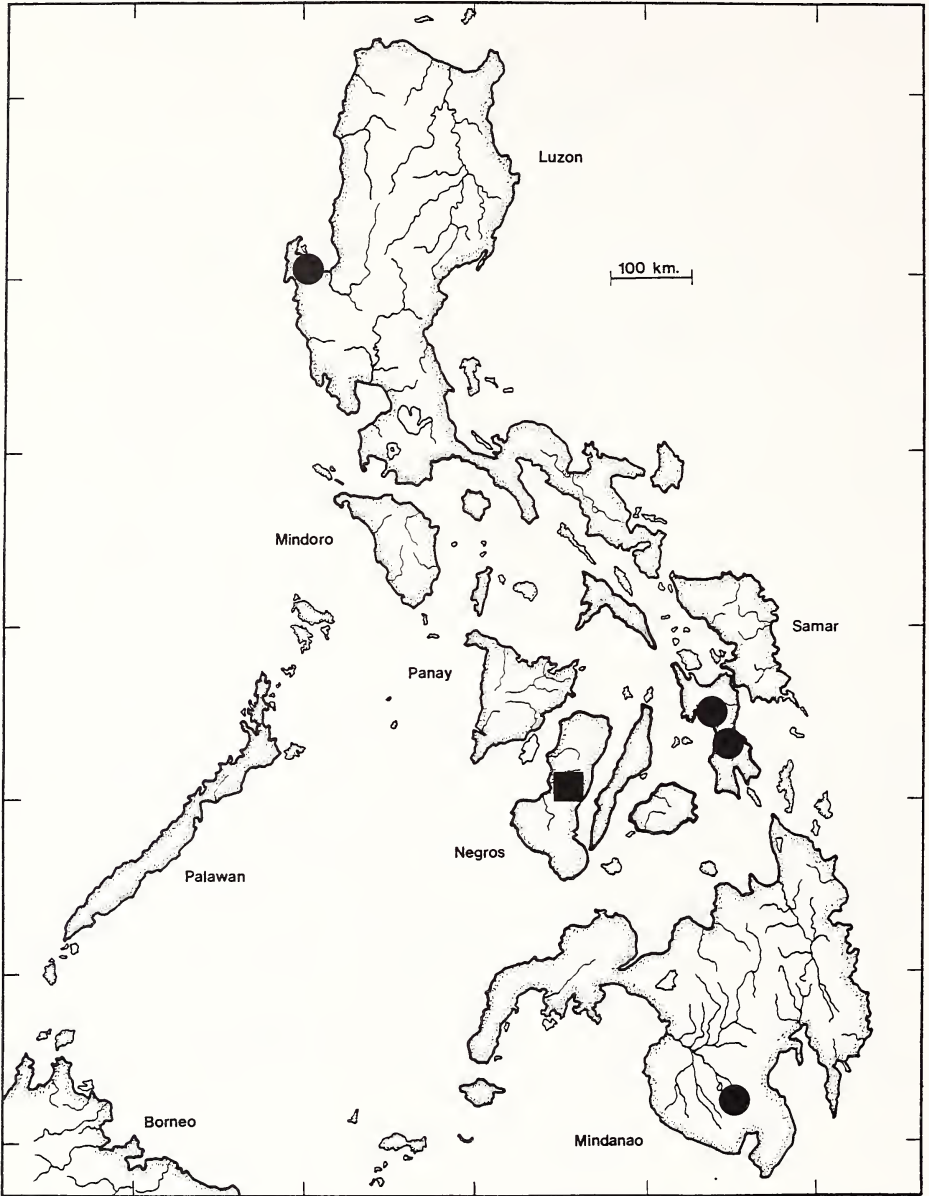


Fig. 9. Distribution of *Rhagovelia* species in the Philippines. Circles = *R. ridicula* n. sp. Square = *R. phoretica* n. sp. (exact location of type locality within island uncertain).

Venter dark grey, weakly overlain with silvery pruinosity; mesosternum, metasternum and abdominal ventrites lacking small black denticles; mesosternum with incipient triangular sulcus centrally; metasternum roughly trapezoidal; abdominal ventrite I narrow, lying in semi-vertical orientation, abdominal ventrites II–VI bulging and tumescent, lacking a longitudinal medial carina; ventrites IV–VI thickly set with long semi-erect pale setae directed posteriorly, ventrite VII with a sharp longitudinal medial carina, this carina continuing onto ventrite VIII and widening posteriorly; segment VIII (first genital segment) stout, not constricted basally; proctiger and genital capsule retracted into segment VIII, proctiger without basal lobes, distal cone coming to a broad but distinct angle; paramere falciform, shape as shown in Figure 5.

Wingless female: Length 3.36 mm; maximum width (across pronotum) 1.36 mm.; body shape as in Figure 1. Similar to wingless male in general structure and coloration with the following exceptions: lengths of antennal segments I–IV = 0.80, 0.44, 0.48, 0.48; extreme posterior margin of mesonotum visible behind posterior margin of pronotum; metanotum tumid at anterolateral angles, these swellings covered with numerous long erect black setae; connexival margins evenly converging adjacent to abdominal tergites I–V, meeting over tergite VI, then diverging slightly over tergites VII–VIII, completely covering tergites VI–VII when viewed from above; abdominal segment VII forming an elongate cylinder, with posterolateral angles produced into long projections, bearing numerous long dark setae (Fig. 2), similar setae also present along posterior margins adjacent to genital cavity; posteromedial portion of abdominal tergite VII produced to a vertical, finger-like process, projecting upward between connexival margins and bearing a fan-like fringe of setae at the apex (Fig. 2); proctiger vertical, gonocoxae recessed into abdominal segment VII, not evident; thoracic and abdominal venter lacking black denticles, abdominal ventrites lacking longitudinal medial carinae or long pale setae; hind femur not incrassate, bearing at most a single small black spine near middle.

Winged male: Length 3.16 mm., maximum width (across humeral angles) 1.37 mm. Similar to wingless male in general structure and coloration with following exceptions: pronotum expanded, length/width = 1.56/1.69, black, with anterior band silvery pruinose and bearing a small dark orange spot centrally behind head vertex, humeral angles prominent, central section tumid, posterior lobe produced to cover entire metanotum, apex coming to a broadly rounded angle, not elevated or prolonged; hemelytra exceeding tip of abdomen, bearing 3 closed cells, with 2 long cells originating in basal portion of the plus another cell in the outer portion of the distal half between the radius and the subcosta; hemelytra uniformly dull black, with basolateral cell between subcosta and radius weakly pruinose; dorsal abdominal carinae moderately long, extending to posterior margin of tergite II; hind femur with armature similar to wingless form.

Winged female: Length 3.46 mm., maximum width (across humeral angles) 1.28 mm. Similar to winged male in general structure and coloration with following exceptions: pronotum length/width = 1.75/2.23; abdomen lacking vertical projection formed by tergite VII as seen in wingless form, connexiva more widely separated, revealing all abdominal tergites when viewed from above with wings removed.

Discussion: *Rhagovelia ridicula* is a member of the *orientalis* group as defined by Polhemus and Polhemus (1988), and is closely allied to *Rhagovelia aberrans* An-

dersen. The two species may be separated by the following characters: the posterolateral connexival angles are prolonged in *ridicula* and bear long hair tufts, while in *aberrans* they are unmodified (compare Figs. 2 and 3); the vertical projection on female abdominal tergite VII emerges from between the connexival margins near the middle of segment VII in *ridicula*, but near the posterior end of the connexiva in *aberrans* (compare Figs. 2 and 3); the basal portions of the connexival margins in *aberrans* bear a thick fringe of erect black setae that is absent in *ridicula*; the posterior margin of abdominal tergite III bears a fringe of scattered long black setae in *aberrans* that is lacking in *ridicula*; and the male parameres of the two species are differently shaped (compare Figs. 4 and 5).

Ecological notes: The Sapa River at the type locality was a slow, shaded stream flowing in a muddy bed, and surrounded by numerous habitations and rice fields. This type of habitat may not be obligatory for *R. ridicula*, however, since it was also taken from swift, rocky streams entering the sea on Luzon and Leyte, and from the clear, rocky Hilusig River, an upland stream on Leyte. All of the localities from which *R. ridicula* is presently known lie in areas in which the original forest has been heavily disturbed or converted over to agriculture, and it is possible that this species has eluded collection up to now due to its preference for disturbed habitats considered worthless by most collectors.

On Luzon *R. ridicula* was taken sympatrically with *R. luzonica* Lundblad, *R. minuta* Lundblad, and *R. cotabatoensis* Hungerford and Matsuda. On Leyte and Mindanao, by contrast, this species was found to be sympatric with *R. usingeri* Hungerford and Matsuda, and *R. orientalis* Lundblad.

Etymology: The name "ridicula" refers to the odd and amusing abdominal modifications exhibited by this species.

Material examined: *Holotype*, wingless female: PHILIPPINES, Mindanao, **South Cotabato Prov.**, Sapa River, SE of Koronadal, 550 m, 20 July 1985, CL 1994, D. A. and J. T. Polhemus (BPBM). *Paratypes*: PHILIPPINES, Mindanao, **South Cotabato Prov.**: 1 winged female, 22 wingless males, 47 wingless females, same data as holotype (BPBM, JTPC). Leyte, **Leyte Prov.**: 3 wingless males, 9 wingless females, Lusig River at Hilusig, 15 July 1985, CL 1979, D. A. and J. T. Polhemus (JTPC); 1 winged female, 10 wingless males, 15 wingless females, Cabigaan River, S. of Ormoc, sea level, 17 July 1985, CL 1987, D. A. and J. T. Polhemus (JTPC). Luzon, **Pangasinan Prov.**: 1 winged male, 12 wingless males, 7 wingless females, stream 6 km. W. of Sual, sea level, 6 July 1985, CL 1956, D. A. and J. T. Polhemus (JTPC).

Rhagovelia aberrans Andersen

Figs. 3, 4

Discussion: *Rhagovelia aberrans* was originally described from Zamboanga, Mindanao, (Andersen, 1965), and the excellent figures accompanying the description illustrate all the salient morphological features of this species. Despite extensive recent collections in the Philippines this species has not been taken outside the Zamboanga Peninsula, indicating that it may be endemic to this area.

Ecological notes: A series of this species was taken by the author and J. T. Polhemus from the Ayala River, a large, unshaded, rocky river flowing swiftly into the sea

northwest of Zamboanga City. This habitat was very similar to localities on Luzon and Leyte from which *R. ridicula* had been taken (see above), and indicates that both of these species may have a preference for swift, open lowland streams.

Material examined: PHILIPPINES, Mindanao, **Zamboanga del Sur Prov.:** 10 wingless males, 23 wingless females, Ayala River at San Ramon, 24 km NW of Zamboanga City, 23 July 1985, CL 1999, D. A. and J. T. Polhemus (JTTC); 1 wingless male, 1 wingless female, Zamboanga, mountain stream, 27 Feb. 1914, T. Mortensen (paratypes, JTTC).

***Rhagovelia phoretica*, new species**

Figs. 6, 7, 9

Diagnosis: Immediately recognizable among Philippine *Rhagovelia* by the broad and ovate form (Fig. 6), sexual dimorphism in body size, with males being much smaller than females, short pronotum with a length at the midline subequal to the length of an eye, and the small, ovate male paramere (Fig. 7).

Description:

Wingless female: Form broadly ovate (Fig. 6), length 3.48 mm; maximum width (across basal abdomen) 1.64 mm. General dorsal coloration dark blackish grey, with basal portions of legs yellowish brown.

Head dark blackish grey, eyes black, frons and vertex bearing scattered stiff black setae; antennae black, segment curved, I thicker than II, all segments covered with very short semi-recumbent dark pubescence, segment I also bearing 3–4 long stiff erect black setae; lengths of segments I–IV = 0.60, 0.36, missing, missing; proepisternum and jugum lacking black denticles.

Pronotum dark blackish grey, short, length/width = 1.12/0.24, broadly exposing mesonotum, posterior margin weakly bisinuate; exposed portion of tumid to either side of depressed midline, length along midline = 2.00, posterior margin biconvex posteriorly; metanotum with anterolateral portions moderately tumid, bearing scattered erect black setae, length along midline = 0.12; entire thoracic dorsum nearly bare, bearing only widely scattered very short recumbent pale setae, with a few longer stout erect black setae on pleural region.

Abdomen dark blackish grey, tergites I–VI subequal in length (0.16, 0.20, 0.20, 0.24, 0.20, 0.24 respectively), tergite VII longer (0.32), tergite VIII shorter than VII (0.28); tergites nearly bare, with only widely scattered very short recumbent pale setae, connexival segments more thickly covered with moderate length semi-recumbent pale setae.

Legs black, with all coxae, fore and hind trochanters, and basal half of fore femur yellowish brown; all segments thickly covered with short recumbent pale setae; trochanters unarmed; fore, middle and hind femora and tibiae with scattered long erect stout black setae along anterior margins; fore femur with scattered slender erect black setae along posterior margin; fore tibia cylindrical, weakly curved and slightly more setiferous distally; middle femur unmodified, cylindrical, tapering, bearing a few long slender erect black setae along posterior margin; middle tibia slender, cylindrical; hind femur with a few scattered long fine erect dark setae along posterior margin, not incrassate, unarmed; hind tibia straight, cylindrical, unarmed.

Proportions of female legs as follows: fore femur/tibia/tarsal 1/tarsal 2/tarsal 3 =

0.98/0.96/0.04/0.04/0.28; middle femur/tibia/tarsal 1/tarsal 2/tarsal 3/ = 1.40/1.20/0.04/0.52/0.84; hind femur/tibia/tarsal 1/tarsal 2/tarsal 3 = 1.00/1.40/0.04/0.05/0.40.

Venter grey; mesosternum, metasternum and abdominal ventrites lacking small black denticles; mesosternum without incipient triangular sulcus centrally; metasternum trapezoidal, unmodified; abdominal ventrite I flat, lying in horizontal orientation, abdominal ventrites II–VII lacking long setiferation or medial carinae; gonocoxae broadly exposed; proctiger lying in a semi-horizontal orientation.

Wingless male: Length 2.48 mm.; maximum width (across pronotum) 1.16 mm. Similar to wingless female in general structure and coloration with the following exceptions: body size much smaller, not as broadly ovate; dorsum of thorax and abdomen thickly covered with short, semi-recumbent dark setae; lengths of antennal segments I–IV = 0.40, 0.32, missing, missing; abdominal tergites I–III equal in length (0.12), IV and V equal in length but longer than preceding (0.14), VI and VII increasingly longer (0.16, 0.24 respectively), VIII shorter than VII (0.16); fore femur and tibia moderately bowed, modified for phoresy; proctiger with basal section bearing weakly produced lateral lobes, distal section with incipient lateral lobes but otherwise unmodified; paramere small, roughly ovate (Fig. 7).

Winged forms: Unknown.

Discussion: *Rhagovelia phoretica* n.sp. belongs to a distinctive intrageneric species group, referred to subsequently as the *caesius* group, that also contains *R. caesius* Lansbury from eastern New Guinea, and is defined by the following characters: strong sexual dimorphism, with males much smaller than females; a broad and ovate overall shape, with silvery grey ground coloration; a short and posteriorly sinuate pronotum in wingless forms; a tumid and broadly exposed mesonotum in wingless forms, with the posterior margin generally bilobate; a small, ovate male paramere; a simple and unmodified proctiger; and slender male forelegs, with the fore tibia curved and modified for grasping. Although the two above taxa are the only members of this assemblage presently described, a large number of additional undescribed species in this clade are present on New Guinea, and will be treated in a monograph on the Melanesian fauna that is currently in progress. The sister area relationship between the Philippines and New Guinea indicated by the distribution of species in the *caesius* group is consistent with the narrative zoogeographical analysis presented by Polhemus and Polhemus (1988) in their monograph of the eastern Indonesian *Rhagovelia* fauna.

Intermixed among the type series from Negros are three specimens (two males and one female) bearing the data "PHILIPPINES, Todaya, Is. Mindanao, July 30, 1970, M. Sato." It seems possible that these specimens were mislabelled, and they are thus not included as paratypes. The Mindanao record for this species, if in fact valid, needs to be reconfirmed.

Hological notes: The type series was taken in company with *Rhagovelia usingeri* Hungerford and Matsuda, but no information is available regarding the specific habitat.

Etymology: The name "phoretica" refers to phoretic modifications of the males for riding on top of the females.

Material examined: *Holotype*, wingless female: PHILIPPINES, Negros, **Prov. uncertain**, Amulan, 16–18 July 1970, M. Sato (BPBM). *Paratypes*: PHILIPPINES,

Negros: 11 wingless males, 12 wingless females, same data as holotype (BPBM, JTTC).

Rhagovalia weneri Hungerford and Matsuda
Fig. 8

Discussion: This species was originally described from high elevation on Mt. Apo, behind Davao, and to date no additional series have been taken. *R. weneri* is of interest in a zoogeographical context because of the structure of the male paramere, which possesses a distinctive, distally spatulate shape typical of the *novacaledonica* group as defined by Polhemus and Polhemus (1988) (Fig. 8). These authors had in fact suggested that *R. weneri* might be a member of this species group, but did not include it as such, since their primary diagnostic character for inclusion involved wing venation, and no winged specimens of *weneri* were available to them. Subsequent analysis of paramere shapes within the Melanesian and Philippine *Rhagovalia* faunas has shown that the spatulate paramere is a strong synapomorphy uniting the species of the *novacaledonica* group, and argues for the placement of *weneri* within it. In addition to *R. weneri*, this paramere shape is seen in all species from New Caledonia, and in a diverse complex of species (including *R. thysanotos* Lansbury, *R. crinita* Lansbury, *R. aureospicata* Lansbury, *R. herzogensis* Lansbury and many additional undescribed taxa) that has radiated in the highlands of New Guinea. Polhemus and Polhemus (1988) proposed a pattern of faunal relationship in which New Caledonia was an ancient continental source area for *Rhagovalia* species occurring on the younger islands of New Guinea and the Philippines, and the distribution of the *novacaledonica* group as now understood supports this hypothesis (Fig. 10), although in a somewhat revised geological context (see following discussion).

The suggestion by Polhemus and Polhemus (1988) that a second Philippine species, *R. hoogstraali* Hungerford and Matsuda, might also be assignable to the *novacaledonica* group, is not supported by the current analysis of paramere shapes. The wing venation in this species is still unknown, however, so its group affinities remain uncertain.

Material examined: PHILIPPINES, Mindanao, **Davao Prov.:** 6 wingless males, 2 wingless females, Sibulan River, Mt. Apo, 7,000–8,000 ft, 21 Sept., C. S. Clagg (JTTC); 1 wingless male, 1 wingless female, E. slope Mt. Apo, stream through original forest, 6,000 ft, November 1946, H. Hoogstraal and F. G. Werner, CHNM-Philippine Zool. Exp. (paratypes, JTTC).

ZOOGEOGRAPHY

The Philippine islands comprise a complex amalgamation of island arcs whose geological history is still poorly understood. Although certain of these arcs, such as the Sulu, Palawan, and Sangihe, may be identified as discrete systems where they emerge from the tectonic knot in the center of the archipelago, others, such as the Negros arc and the accreted terranes of the Pacific Cordillera along the east coast of Mindanao, are much more difficult to interpret. At least six accreted arc systems are present in this region (Hamilton, 1979, 1989; see figs. 79, 99, 111 in the former work), and much additional onshore geology remains to be done before the history of the area can be properly comprehended.

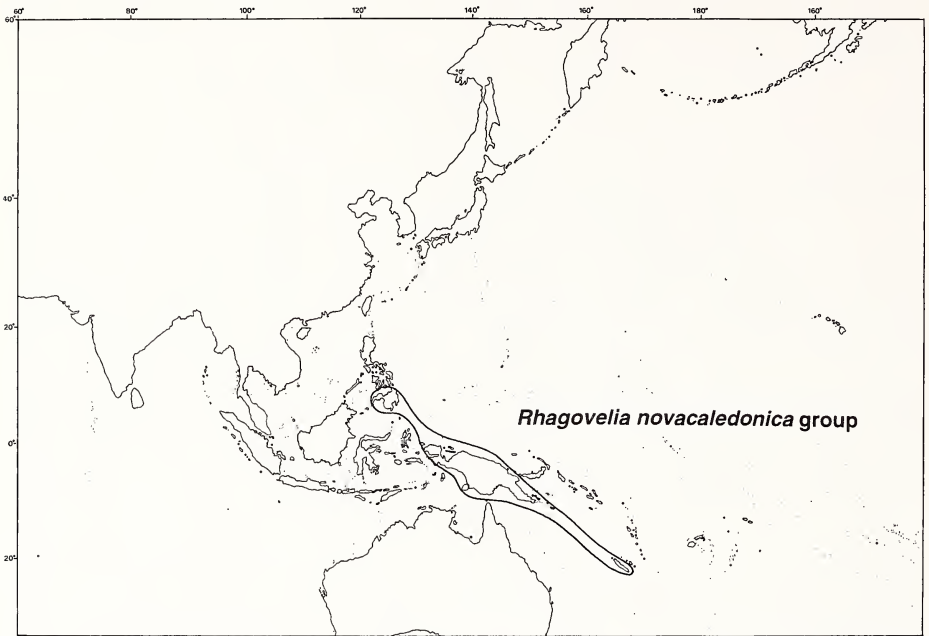


Fig. 10. Distribution of the *Rhagovelia novacaledonica* group.

The complex geology of the Philippine archipelago is reflected in the multicentric origins of its *Rhagovelia* biota, which shows alliances to disjunct groups of species occurring on Borneo, Celebes, and New Guinea. The patterns involving the former two areas were discussed in detail by Polhemus and Polhemus (1988) in their monograph on the *Rhagovelia* of eastern Indonesia, while the linkages to New Guinea were alluded to but not treated in detail. The present study illustrates much more conclusively the presence of distinctively Papuan *Rhagovelia* species groups in the southern and central Philippines, and raises the question of how such patterns were established.

Similar sister area relationships between the Philippines and New Guinea are also seen in other families of aquatic Heteroptera. Polhemus and Polhemus (1987) noted that sagocorine Naucoridae were found in both regions, but not in the intervening northern Moluccas or Celebes, a pattern apparently identical to that displayed by the *caesius* and *novacaledonica* species groups in *Rhagovelia*. In both this and the previously cited study the authors concluded that the Philippines and New Guinea represented sister areas for certain groups of aquatic Heteroptera, and postulated that a tectonic mechanism was responsible for this faunal disjunction. No simple geological explanation was evident, however, and at the time the authors had insufficient knowledge of regional tectonics to suggest any mechanistic hypothesis.

The present study further clarifies the linkages between certain elements of the Papuan and Philippine *Rhagovelia* biotas. In addition, a more thorough knowledge of regional geology now allows a mechanistic hypothesis to be advanced that would explain this pattern. It is proposed herein that a subsequently displaced, eastward

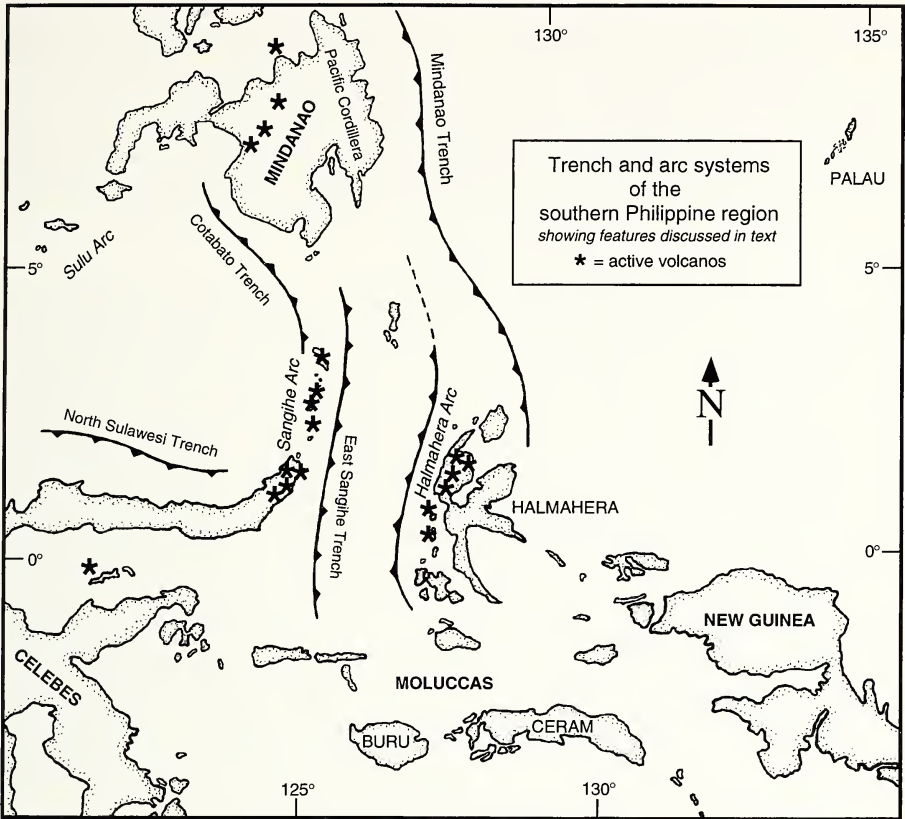


Fig. 11. Map showing selected tectonic elements in the southern Philippine and Molucca Sea regions, including island arcs discussed in the text (after Hamilton, 1979).

migrating arc system once contributed faunal elements to both the southern Philippines and New Guinea. This arc was probably not the system that was accreted to the northern margin of New Guinea in the Miocene, forming the present north coast ranges, because this Miocene arc harbored certain Asian aquatic Heteroptera groups, such as the genus *Ptilomera*, which are absent in the Philippines outside the Palawan arc. Nor was it part of the Sangihe or Halmahera arcs that were initiated in the Eocene and are presently colliding in the Molucca Sea (Fig. 11). Instead, this arc was probably part of a long, pre-Eocene, northwest-southeast trending system that once extended from New Zealand and New Caledonia through the Solomon region, past the section of northern Australia that would later become New Guinea, and onward to what is now Mindanao.

Portions of this pre-Eocene arc may be represented along the northern flank of the New Guinea central highlands in the Jimi Terrane. This anomalous crustal block contains Mesozoic volcanic rocks that appear to be the result of arc magmatism (Hamilton, 1979), but its tectonic histories are poorly understood. This terrane could

have attained its present juxtaposition by arc collision with the stable northern Australian continental margin in the Mesozoic, or could have formed offshore and have been incorporated into an advancing arc that subsequently collided with New Guinea in the Miocene (for CD-ROM video reconstruction of tectonic events in eastern New Guinea see Yan and Kroenke, 1994). Hamilton (1979) postulated that this terrane might be correlative with the eastern Australian tectonic and magmatic belts of Cretaceous age, which formed about the same time that New Caledonia migrated away from the eastern Australian continental margin (Kronke, 1984); Hamilton's suggestion is thus compatible with the zoogeographical pattern displayed by the *novacaledonica* species group of *Rhagovelia* (Fig. 10).

Arc-related materials of Cretaceous age are also present in southern Mindanao (Hamilton, 1989), and their existence is consistent with the above pre-Eocene arc hypothesis, but little is known regarding the history of these Mesozoic arc systems or whether the terranes derived from them are correlative to the Cretaceous emplacements in central New Guinea. The Pacific Cordillera of Mindanao also contains ophiolites and other remnants of more recently collided arc systems, which have been interpreted by Hamilton (1979) and subsequent workers to represent the on-shore remnants of the convergent Halmahera and Sangihe arcs, which sutured along their northern sectors in the middle Tertiary (Hawkins et al., 1985), and have been subsequently overprinted by products from the more recently initiated Mindanao Trench system (for geographical locations of these tectonic structures see fig. 10). If either of these latter two arcs had provided a means for faunal interchange between New Guinea and the Philippines, either as dispersal corridors or tectonic rafts, then one would also expect to see remnant taxa from some of the groups involved represented in the faunas of the northern Moluccas or northern Sulawesi as well. Several aquatic Heteroptera surveys in these latter islands over the last ten years, however, including one by the author and J. T. Polhemus in 1985, have produced no collections of the groups involved in the New Guinea-Philippine disjunction. Rather than providing a linkage to New Guinea, the Sangihe Arc is currently allowing faunal interchange between Mindanao and Celebes, as demonstrated by the distribution of the *orientalis* group (Polhemus and Polhemus, 1988, and examples herein). This arc has moved eastward with time (Hamilton, 1989), and members of the *orientalis* group distributed along it have not yet reached the Moluccas or New Guinea. I hypothesize that Sangihe arc is in fact a relatively recent faunal conduit, and that the direction of *Rhagovelia* migration along it has been from the Philippines southward into Celebes, because the former area contains a diverse assemblage of species in the *orientalis* group, while the latter island has so far yielded only three (Polhemus and Polhemus, 1988; Nieser and Chen, 1993).

If a Paleocene arc did in fact formerly link the Philippines and New Guinea, then the central sector of this system must have either migrated or been displaced prior to the development of the convergent Sangihe and Halmahera arc systems, the former of which is apparently of Eocene age (Weissel, 1980). The displacement of this older arc could have occurred along the Sorong Fault, a major left-lateral system that cuts across the extreme western tip of northern New Guinea, and has apparently transported continental fragments from the Vogelkop Peninsula eastward to near Celebes, but this is not supported by biological evidence. Conversely, fragments of this older arc could have been carried northwestward along strike-slip faults bound-

ing the western margin of the Pacific Plate, in a manner similar to that seen in the vicinity of present day New Ireland. Present plate motions and the apparent youth of the Mindanao Trench (Hamilton, 1979; Kroenke, 1984) are consistent with such a hypothesis of previous left-lateral shear in this region. Further collections of aquatic Heteroptera on the arc islands between Celebes, the Philippines and New Guinea, combined with additional geological investigations in the southern Philippines, will be necessary before these hypotheses can be more critically evaluated.

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